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Contributed Paper

Inferring Extinction of Mammals from Sighting Records, Threats, and Biological Traits

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Abstract: *For species with five or more sightings, quantitative techniques exist to test whether a species is extinct on the basis of distribution of sightings. However, 70% of purportedly extinct mammals are known from fewer than five sightings, and such models do not include some important indicators of the likelihood of extinction such as threats, biological traits, search effort, and demography. Previously, we developed a quantitative method that we based on species' traits in which we used Cox proportional hazards regression to calculate the probability of rediscovery of species regarded as extinct. Here, we used two versions of the Cox regression model to determine the probability of extinction in purportedly extinct mammals and compared the results of these two models with those of stationary Poisson, nonparametric, and Weibull sighting-distribution models. For mammals with five or more sightings, the stationary Poisson model categorized all but two critically endangered (flagged as possibly extinct) species in our data set as extinct, and results with this model were consistent with current categories of the International Union for the Conservation of Nature. The scores of probability of rediscovery for individual species in one version of our Cox regression model were correlated with scores assigned by the stationary Poisson model. Thus, we used this Cox regression model to determine the probability of extinction of mammals with sparse records. On the basis of the Cox regression model, the most likely mammals to be rediscovered were the Montane monkey-faced bat (*Pteralopex pulchra*), Armenian myotis (Myotis hajastanicus), Alcorn's pocket gopher (*Pappogeomys alcorni*), and Wimmer's shrew (*Crocidura wimmeri*). The Cox model categorized two species that have recently disappeared as extinct: the baiji (*Lipotes vexillifer*) and the Christmas Island pipistrelle (*Pipistrellus murrayi*). Our new method can be used to test whether species with few records or recent last-sighting dates are likely to be extinct.*

Keywords: Cox proportional hazards regression, rediscovery, Solow equation

Infiriendo la Extinción de Mamíferos a Partir de Registros Visuales, Amenazas y Atributos Biológicos

Resumen: *Existen técnicas cuantitativas para especies con cinco o más avistamientos que permiten probar si una especie está extinta con base en la distribución de avistamientos. Sin embargo, 70% de las especies de mamíferos supuestamente extintas son conocidas con menos de cinco avistamientos, y tales modelos no incluyen algunos indicadores importantes de la probabilidad de extinción, como amenazas, atributos biológicos, esfuerzo de muestreo y demografía. Previamente, desarrollamos un método cuantitativo que basamos en los atributos de las especies y en el que utilizamos la regresión de Cox para riesgos proporcionales para calcular la probabilidad de redescubrimiento de especies consideradas extintas. Aquí, utilizamos dos versiones del modelo de regresión de Cox para determinar la probabilidad de extinción de mamíferos supuestamente extintos y comparamos los resultados de estos dos modelos con los del modelo estacionario de Poisson, no paramétrico, y del modelo de Weibull de distribución de avistamientos. Para mamíferos con cinco o más avistamientos, el modelo estacionario de Posisson clasificó como extintas a todas las especies, excepto dos especies en peligro crítico (consideradas como posiblemente extintas), de nuestra base de datos, y los resultados con este modelo fueron consistentes con las categorías actuales de la Unión Internacional para la Conservación de la Naturaleza. Los valores de la probabilidad de redescubrimiento de especies individuales en una versión de*

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nuestro modelo de regresión de Cox se correlacionaron con los valores asignados por el modelo estacionario de Poisson. Por lo tanto, utilizamos este modelo de regresión de Cox para determinar la probabilidad de extinción de mamíferos con registros escasos. Con base en el modelo de regresión de Cox, los mamíferos con mayor probabilidad de ser redescubiertos fueron Pteralopex pulchra*, Myotis bajastanicus,* Pappogeomys alcorni *y* Crocidura wimmeri*. El modelo de Cox clasificó como extintas a dos especies que han desaparecido recientemente:* Lipotes vexillifer *y* Pipistrellus murrayi*. Nuestro nuevo método puede ser utilizado para estimar la probabilidad de extinción de especies con pocos registros o cuya fecha de último avistamiento es reciente.*

Palabras Clave: ecuación de Solow, redescubrimiento, regresión de Cox para riesgos proporcionales

Introduction

Species presumed to be extinct are often rediscovered (approximately 30% of mammals) (Fisher 2011*a*; Fisher & Blomberg 2011). Resources are wasted searching for species that have no chance of rediscovery, but there are no searches for most missing species (Fisher 2011*b*). On the one hand, understanding of the current rate of extinction will be compromised if lists of extinct species have errors of omission. On the other hand, erroneous designation of extinction can lead to the withdrawal of conservation efforts (Collar 1998). Quantitative predictions of which species are most likely to be extinct and which might be rediscovered are therefore needed.

For species with five or more dated sightings, there are well-established techniques to test for extinction. Solow and Roberts used the distribution of sighting records to develop a set of statistical methods that calculates the probability that an undetected species is extinct, estimates the year of extinction, and provides the year of 95% confidence of extinction (Solow 1993*a*, 2005; Roberts & Solow 2003; Solow & Roberts 2003). Following the definitions of Solow (2005), we called dated detections (including captures and specimen-collection dates) *sightings* and the set of sightings for a particular species a *sighting record*.

In the stationary Poisson model (often called the Solow equation), the distribution of intervals between successive sightings of the species before its last record, and the gap between the last record and the present are used to calculate the probability that the gap between the last record and the present is within the same distribution of sighting intervals as the historical sighting record. In the stationary Poisson model it is assumed that there is no systematic trend in the likelihood of detection over time because search effort and abundance are constant before the species declines suddenly to extinction. Although these assumptions have been called restrictive and unrealistic (Rivadeneira et al. 2009), the results of several recent studies show this model is widely applicable. It gives realistic results for species that declined rapidly (e.g., when a species with a small range is extirpated by a predator or disease) or for species that were sighted toward the end of their decline and thus had a brief record of decline (Rout et al. 2009). The model is expected to work best when the species is unmonitored (sightings are opportunistic) or monitored with replicated surveys (Solow 1993*a*).

An advantage of the stationary Poisson model is that it produces relatively narrow confidence intervals. Elphick et al. (2010) used this model and found that the time between mean last sighting dates of North American and Hawaiian birds and their estimated extinction dates was only four years. Vogel et al. (2009) used quantitative goodness-of-fit tests to show that sighting records of 24 out of 27 undetected North American and Hawaiian birds conformed best to the stationary Poisson model, rather than alternative models. The most likely violation of model assumptions in historical data sets is increasing detection probability over time due to an increased interest in finding rare species, increased number of researchers, and improved equipment and ability to access isolated regions (Elphick et al. 2010; Roberts et al. 2010).

In simulations, the stationary Poisson model yields reliable results when sighting rates increase before the true extinction date (Rivadeneira et al. 2009). In a modification of the stationary Poisson model, McCarthy (1998) accounted for changing survey effort across the sighting record. He applied both the modified and original versions of the stationary Poisson model to a museum collection of southwestern Australian mammals, in which collection effort was increasing, and found that both models perform well. If the sighting rate before extinction declines rather than increases, then the stationary Poisson approach yields premature extinction dates, increasing the type I error rate (incorrectly concluding that a species is extinct). Solow (1993*b*) developed the nonstationary Poisson model for use with species that decline steeply to extinction. However, this model has low power if extinction is recent or if sighting rate is very low and requires a long record of sightings to approximate a continuous distribution. In addition, the upper bound of the 95% CI can be impossible to calculate (Solow 2005).

The Weibull model is based on a subset of the most recent sightings of an undetected species. Assumptions of this model are that these sightings are the latest in a much longer record and the sighting record has reached an asymptote (Solow 2005). Unlike with the stationary Poisson model, it is not assumed that detection probability or abundance prior to extinction is stable (they may

be declining), but because this model does not use all possible data, confidence intervals around the estimated extinction date are relatively wide (Solow 2005). Vogel et al. (2009) found that the distribution of the asymptotic extreme value of the Weibull model was generally not a good approximation for the brief sighting records of putatively extinct North American and Hawaiian birds (6–28 sightings per species), in contrast to the stationary Poisson model. Rivadeneira et al. (2009) found that unlike the stationary Poisson model, the Weibull model predicts extinction dates with 95% confidence in simulations, even when decline is gradual and sighting probabilities are low, but that frequent type II errors (an extinct species is considered extant) are likely.

The nonparametric model is based only on the two sightings before extinction (Solow & Roberts 2003). Because it uses so little of the potential data, no assumptions are made about the evenness of the sighting rate other than the rate is smooth and positive at the end of the observation period (Solow & Roberts 2003). However, this model produces large confidence intervals and is inefficient (Solow 2005). As with the Weibull model, Rivadeneira et al. (2009) found that the nonparametric model usually predicts extinction dates with 95% confidence in simulations, even when decline is gradual and sighting probabilities are low, but that the probability of type II errors is greater than with the stationary Poisson model.

Models that are based on sighting records do not include some important indicators of probability of extinction, such as survey or collection effort, species' conspicuousness and biological traits, and known threats to the species (Butchart et al. 2006; Fisher & Blomberg 2011). Thus, Elphick et al. (2010) suggested that these models alone should not be relied on to determine extinction. We previously developed Cox proportional hazards regression models to test how different biological variables and threats affect the probability of rediscovery in mammals (Fisher & Blomberg 2011).

We found that the rate of rediscovery is lowest in mammals with small geographic ranges affected by invasive predators, species that were harvested to apparent extinction in the 19th century, species for which recent, intense search efforts have been unsuccessful, and species with formerly high population densities. In this study, we used these models to estimate the probability that particular undetected species are extinct on the basis of the mean rediscovery-rate curve for a species' specific combination of traits and the time since it was last recorded. This method requires a record of the last sighting of an undetected species to estimate the probability of rediscovery and the probability of the species remaining undetected (or being extinct). In the Cox proportional hazards regression model, no particular underlying extinction time distribution is assumed, so the results of the Cox model are not affected by the rate of decline before extinction or the stability of effort between sightings. Other assumptions of this method are that the date of the last sighting, key species traits, and the general cause of decline are accurately known and that correlates of the probability of rediscovery in the past will be predictive in the future.

Here, we used the stationary Poisson, Weibull, and nonparametric sighting-distribution methods to determine whether undetected mammals with a sufficient number of records are likely to be extinct (>4 records for the stationary Poisson and Weibull models, >2 for the nonparametric model). We used two versions of our Cox regression model (Fisher & Blomberg 2011) to calculate the relative probability that undetected species of mammals will be rediscovered. We sought to evaluate the performance of our methods relative to sighting distribution models to determine whether Cox models can be used to test extinction in species with few dated sighting records. We also aimed to identify which undetected mammal species are probably extinct and which are most likely to be rediscovered.

Methods

To analyze dates of past records of undetected species for sighting distribution models and species rediscovery rates for Cox regression models, we assembled a global database of species with long gaps in their sighting records (i.e., researchers reported that gaps were long enough to suspect extinction). We included species reported as extinct (including species on the International Union for Conservation of Nature [IUCN] Red List categorized as extinct, critically endangered possibly extinct, or extinct in the wild) and species considered undetected according to the literature (Fisher & Blomberg 2011). To establish the status and detection history of these species, we used IUCN Red Lists and related publications, primary literature, books, museum records, and databases, including the Global Biodiversity Information Facility Data Portal (2010), OZCAM (2010), and NatureMap (2010), and the Mammal Database (MacPhee & Flemming 1999*a*, 1999*b*).

In Fisher and Blomberg (2011), we classified each species as either currently undetected or extinct, or rediscovered, and recorded the date of last sighting before the species was considered extinct and rediscovery (if rediscovered). We did not include unsubstantiated rediscoveries and sightings that lacked physical evidence of taxonomic identity to species (e.g., Baillie et al. 2009). We did not include five extinct species (*Coryphomys buehleri*, *Hippopotamus lemerlei*, *Hippopotamus madagascariensis*, *Palaeopropithecus ingens*, and *Prolagus sardus*) on the 2009 IUCN Red List that are known from subfossil material (skeletal remains)

because their key traits, such as body size and distribution, are unknown. Not including species that are extinct in the wild (and exist only in captivity or in reintroduced populations), Fisher and Blomberg (2011) identified 116 mammals that have been considered extinct or possibly extinct (67 of which have been rediscovered) and assembled a database of the traits of these species (threatening factors, geographic range, search effort after the species was reported undetected, population density, elevation, habitat openness, island dweller or not, body mass, color, arboreality, diurnality, gregariousness, and mean human population density within range).

Cox Models

Previously (Fisher & Blomberg 2011), we used Cox regression to examine the effect of undetected species' traits on the likelihood of rediscovery (Therneau & Grambsch 2000). We modeled the annual persistence of extinct status with respect to potential covariates (i.e., rediscovery is analogous to death in a survival model, in which mean survival is compared among groups with different traits, and the result is expressed as a mean survival curve for each group). The Cox proportional hazards regression model is specified as

$$\lambda_i(t) = \lambda_0(t)e^{\mathrm{X}_i(t)\beta}, \tag{1}$$

where $\lambda_i(t)$ is the hazard of rediscovery for the ith species at time t, $\lambda_0(t)$ is the baseline (empirical) hazard function, $\mathrm{X}_i(t)$ is a vector of covariate values for the ith species (i.e., species' traits, including threats and search effort), and β is a vector of slope coefficients to be estimated. This semiparametric model has an advantage over the usual parametric approach to time-to-event modeling in that the form of the baseline hazard function does not have to be specified. It is assumed (Grambsch & Therneau 1994) that the ratio of the hazards for two species with different covariate values is constant over time. That is, for two species i and j

$$\frac{\lambda_i(t)}{\lambda_j(t)} = \frac{\lambda_0(t)e^{\mathbf{X}_i(t)\beta}}{\lambda_0(t)e^{\mathbf{X}_j(t)\beta}} = \frac{e^{\mathbf{X}_i(t)\beta}}{e^{\mathbf{X}_j(t)\beta}} \tag{2}$$

is constant.

Estimates of β are obtained by maximizing the partial likelihood (Cox 1972):

$$\mathrm{PL}(\beta) = \prod_{i=1}^{n}\prod_{t\geq 0}\left\{\frac{Y_i(t)r_i(\beta,t)}{\sum_j Y_j(t)r_j(\beta,t)}\right\}^{\mathrm{d}N_i(t)}, \tag{3}$$

where Y_i is an indicator variable for the status of species i (i.e., $Y = 1$, extinct; $Y = 0$, rediscovered) and $r_i(\beta, t) = e^{X_i(t)\beta}$ is the probability of rediscovery of species i. Undetected (presumed extinct) species in our data set that were not rediscovered by 2010 were considered right-censored at 2010.

Use of Cox Models

First, we tested for associations between species' traits and probability of rediscovery (or remaining in the extinct category) with Cox proportional hazards regression (Fisher & Blomberg 2011). Second, we used the fitted Cox proportional hazards model for each presumed-extinct species to estimate the probability that the species will not be rediscovered (it will remain in the extinct category). No mammal species undetected for >180 years has been rediscovered, so all species undetected for >180 years had an estimated probability of rediscovery of zero. Third, we assumed that no more species would be rediscovered after 180 years; therefore, as the number of years undetected approached 180, the probability of rediscovery approached zero. The shape of the curve (how steeply it approaches the value at 180 years) varied as a function of species' traits. For example, the curve was steep for species with large geographic ranges and shallow for species with very small ranges (Fisher & Blomberg 2011). We estimated the probability that each species would remain in the extinct category with the fitted mean curve for that species; we subtracted the probability of remaining extinct at 180 years from the probability of remaining extinct at the current time (Fig. 1).

The significant species traits and variables in our models were search effort, main cause of decline, century in which the species was no longer detected, range size (in ranked categories), and population density (in ranked categories). In species last seen before the 19th century, there was no variation in search effort and there were no species for which extinction was attributed mainly to habitat loss. Therefore, Fisher and Blomberg (2011) constructed two models: one from a data set that included species from all centuries and the variable search effort (Cox search) and one from a reduced data set that included the 19th, 20th, and 21st centuries, but excluded search effort and species not seen since before the 19th century (Cox century). With the Cox search data set, range rank and search effort were positively correlated with probability of rediscovery, population density was negatively correlated with probability of rediscovery, and the probability of rediscovery was greater for species affected by habitat loss than for those affected by harvesting or introduced predators and diseases (Fisher & Blomberg 2011). With the Cox century data set, the probability of rediscovery was greater for species last seen in the 20th century, especially for those affected by harvesting and those affected by habitat loss that had relatively large ranges (Fisher & Blomberg 2011).

Calculation of Solow Models

Twenty-five species had a record of more than four sightings. For these species, we used the stationary Poisson,

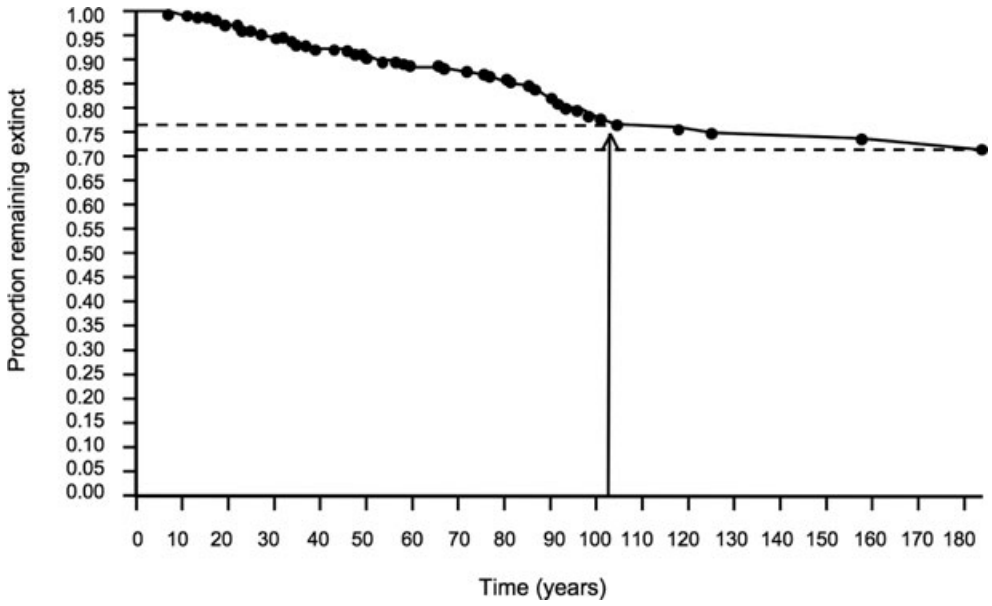

Figure 1. Methods of calculations of probability of extinction in missing species with the Cox regression model. The figure shows the fitted mean Cox regression curve for species with a range size rank 1 (<1 km^2), with low density, that are threatened by habitat loss and for which search effort has been low. At time zero, the probability of species in the data set remaining in the extinct category is 1 (no species have been rediscovered). The proportion of species remaining missing at 180 years is 0.72. The value at 102 years is 0.77 (arrow). After 102 years, 77.3% of species with these traits remain missing, and 5.2% of species with these traits remain to be rediscovered, assuming no rediscoveries occur after 180 years (the maximum time a rediscovered mammal species has been missing).

Weibull, and nonparametric models as described in Solow (2005) to test the null hypothesis that each species is extant. We also applied the nonparametric model to species with three or four sightings (Table 1 & Supporting Information). There is an error in Eq. 18 of Solow (2005) (A.R. Solow, personal communication) that we corrected in our analyses here (exponent in Eq. 18 should not be negative). We use R (R Development Core Team 2009) to perform calculations. The code is available on request.

We found the number of undetected species classified as extant by each model and used Pearson's correlations and Spearman's correlations to compare the results of each model across species.

Results

The stationary Poisson model assigned the most species to extinction ($p < 0.1$), and the Cox century model assigned the fewest species to extinction (Table 1). According to the stationary Poisson model, only two undetected mammals out of 25 with sufficient sighting records had $p > 0.1$. These were the two most recent potential extinctions, the baiji (*Lipotes vexillifer*) (last confirmed sighting 2006) and Alcorn's pocket gopher (*Pappogeomys alcorni*) (last confirmed sighting 1998). Both are listed as critically endangered by the IUCN (Table 1 and Supporting Information). Species' threat categories assigned with the stationary Poisson model were consistent with current IUCN Red List classifications, and this was the only model that distinguished among the red list categories of critically endangered, critically endangered possibly extinct, and extinct (Table 1). This model estimated a p value under the null hypothesis of not extinct of <5% in 18 species classified as extinct by the IUCN (Table 1 & Supporting Information) and a $p = 0.05$–0.10 in two species categorized as critically endangered possibly extinct (the Telefomin cuscus [*Phalanger matanim*] and the kouprey [*Bos sauveli*]) and in three species classified as extinct (the San Quintin kangaroo rat [*Dipodomys gravipes*], greater short-tailed bat [*Mystacina robusta*], and Swan Island hutia [*Geocapromys thoracatus*]).

The Weibull model also classified relatively few undetected species as extant (Table 1). The Weibull and stationary Poisson models categorized the same two species currently considered critically endangered as extant ($p >$ 10%) (Alcorn's pocket gopher and the baiji). The Weibull and stationary Poisson models also both categorized four other recently undetected species as extant ($p > 10\%$). The nonparametric model categorized nine extinct or critically endangered possibly extinct, one critically endangered, and one data deficient species as extant, but Alcorn's pocket gopher had $p = 0.07$ under the null hypothesis of not extinct.

Table 1. Results of all models (Poisson, nonparametric, Weibull, Cox search, and Cox century) of mammal species probability of extinction and significance level of tests for extinction for species with ≥5 sightings.

Species	*StP*[a]	*NP*[b]	*Weibull*[c]	*Cox search*[d]	*Cox cent*[e]	*Last date*[f]	*StP date*[g]
Phalanger matanim, Telefomin cuscus	0.05	0.35	0.82	0.51	0.921	1997	2000
Pappogeomys alcorni, Alcorn's pocket gopher	0.36	0.07	0.11	0.21	0.817	1998	2009
Bos sauveli, kouprey	0.06	0.41	0.63	0	0.706	1986	1993
Lipotes vexillifer, baiji	0.13	0.33	0.31	0	0.972	2006	2007
Dipodomys gravipes, San Quintin kangaroo rat	0.004	0.11	0.02	0.385	0.819	1986	1989
Onychogalea lunata, crescent nailtail wallaby	0.003	0.34	0.08	0.276	0.489	1956	1963
Perameles eremiana, desert bandicoot	0.02	0.15	0.22	0.256	0.430	1943	1954
Geocapromys thoracatus, Swan Island hutia	0.09	0.25	0.32	0.025	0.184	1955	1972
Macrotis leucura, lesser bilby	0	0.08	0.01	0.176	0.535	1931	1937
Mystacina robusta, greater short-tailed bat	0.0001	0.04	0.02	0.112	0.573	1967	1968
Macropus greyi, toolache wallaby	0.0002	0.01	0.001	0.167	0.435	1927	1932
Monachus tropicalis, Caribbean monk seal	0.01	0.06	0.06	0.32	0.568	1952	1960
Rucervus schomburgki, Schomburgk's deer	0.01	0.07	0.06	0.235	0.468	1938	1947
Lagorchestes leporides, eastern hare-wallaby	0	0.008	0.007	0.002	0.125	1890	1898
Rattus macleari, Maclear's rat	0	0.009	0.0007	0.017	0.171	1903	1905
Rattus nativitatis, bulldog rat	–	0.13	–	0.038	0.212	1903	–
Nesoryzomys darwini, Darwin's Galapagos mouse	–	0.01	–	0.126	0.534	1930	–
Thylacinus cynocephalus, thylacine	0	0.03	0	0	0.339	1933	1935
Megalomys desmarestii, pilorie	0.006	0.009	0.004	0.01	0.238	1902	1915
Nesoryzomys indefessus, indefatigable Galapagos mouse	0.01	0.06	0.09	0.019	0.312	1934	1943
Gazella saudiya, Saudi gazelle	–	0.01	–	0.058	0.511	1936	–
Neotoma anthonyi, Anthony's woodrat	–	0.04	–	0.04	0.160	1926	–
Neotoma martinensis, San Martin Island woodrat	–	0.03	–	0.038	0.160	1925	–
Neovison macrodon, sea mink	–	0.09	–	0	0	1880	–
Pteropus subniger, Réunion flying fox	0.02	0.03	0.02	0	0.100	1864	1887
Hydrodamalis gigas, Steller's sea cow	0	0.004	0.003	0	0	1768	1773
Hippotragus leucophaeus, blue buck	0.0001	0.01	0.01	0	0	1799	1805
Dusicyon australis, Falkland Island wolf	0.03	0.04	0.03	0	0.100	1876	1907
Oryzomys antillarum, Jamaican rice rat	–	0.1	–	0.025	0.078	1877	–
Potorous platyops, broad-faced potoroo	–	0.06	–	0	0.000	1875	–
Conilurus albipes, white-footed rabbit-rat	0.01	0.08	0.06	0	0.000	1875	1891
Chaeropus ecaudatus, pig-footed bandicoot	0	0.05	0.004	0.05	0.088	1907	1916
Bos primigenius, aurochs	0	0.01	0.01	0	0	1627	1642

[a] *The* p *values under the null hypothesis of no extinction calculated with the stationary Poisson model.*
[b] *The* p *values under the null hypothesis of no extinction calculated with the nonparametric model.*
[c] *The* p *values under the null hypothesis of no extinction calculated with the Weibull model.*
[d] *Probability of the species being extant (and detected) with the Cox proportional hazards model, with a data set including species from all centuries and variable search effort.*
[e] *Probability of the species being extant (and detected) with the Cox proportional hazards model, with a data set including the 19th, 20th, and 21st centuries, excluding search effort and species not seen since before the 19th century.*
[f] *Date of last sighting.*
[g] *Mean extinction date estimated with the stationary Poisson model.*

Seventy percent of undetected mammal species in our data set (82 species) did not have sufficient data for us to apply the stationary Poisson, nonparametric, and Weibull models. It was not possible to use sighting distribution methods for 20 mammals that became extinct in the 16th century (known from skeletal material with approximate ages only) or for 45 species known from only a single dated sighting. Most of these enigmatic species are known only from a single specimen or series. A few (e.g., the Japanese sea lion [Abe et al. 2008]) were once abundant, but lack multiple published and dated records. Within the set of species with at least five sightings, nine extinct or critically endangered possibly extinct and one critically endangered species were categorized as extant by the Cox search model and 18 were categorized as extant by the Cox century model, including the two critically endangered species. Two-thirds of species for which classification among models did not agree, including the thylacine, were classified as extant by only the Cox century model (Table 1 and Supporting Information).

The p values for Pearson correlations for all three models that were based on sighting records were significantly correlated with probabilities of extinction in the Cox century model. The results of the Weibull model were correlated with those of the Cox search model. However, the results of the stationary Poisson model were not correlated with those of the other sighting distribution models or with those of the Cox search model (Table 2). Spearman rank correlations showed that all models ranked species' probabilities of extinction

Table 2. Correlation matrix showing Pearson correlations and Spearman correlations between significance levels and rediscovery probabilities generated by stationary Poisson[a], nonparametric[b], Weibull[c], Cox search[d], and Cox century[e] models of mammal species extinction.

Correlation and model	*Stationary Poisson*	*Nonparametric*	*Weibull*	*Cox search*	*Cox century*
Pearson					
Stationary Poisson		0.24	0.26	0.09	0.45[a]
Nonparametric			0.83[h]	0.31	0.61[g]
Weibull			–	0.36[f]	0.55[g]
Cox search				–	0.77[h]
Spearman					
Stationary Poisson	–	0.65[h]	0.85[h]	0.13	0.45[f]
Nonparametric		–	0.84[h]	0.42[f]	0.64[h]
Weibull			–	0.28	0.52[f]
Cox search				–	0.60[g]

[a] *Stationary Poisson sighting distribution model (Solow 1993a).*
[b] *Nonparametric sighting distribution model (Solow & Roberts 2003).*
[c] *Weibull sighting distribution model (Solow 2005).*
[d] *Cox proportional hazards model with a data set including species from all centuries and variable search effort.*
[e] *Cox proportional hazards model with a data set including the 19th, 20th, and 21st centuries, but excluding search effort and species not seen since before the 19th century.*
[f] $p < 0.05$.
[g] $p < 0.01$.
[h] $p < 0.001$.

similarly, except for the Cox search model, which yielded relative species ranks that were not correlated with those of the stationary Poisson or Weibull models (Table 2).

Discussion

Evaluation of Models

We expected that the stationary Poisson model would provide the best results for species in our data set with sufficient records, because in potentially extinct birds goodness-of-fit tests indicate that the stationary Poisson model is appropriate for most species (Vogel et al. 2009). This model is most appropriate because it makes efficient use of sighting records and so has the smallest confidence intervals. Provided a species is not declining steeply throughout the sighting record, the model has a low rate of erroneously classifying extinction (type I error). Rivadeneira et al. (2009) also found that the stationary Poisson model has a lower rate of type II error (failing to correctly classify extinction) than either the Weibull or nonparametric models. Our results appear to be consistent with this because the Weibull and nonparametric models classified 20% and 28% of undetected species with sufficient records as extant ($p \geq 0.9$) in contrast to the stationary Poisson model, which classified 8% of species as extant. Our data should also be appropriate for the stationary Poisson model because, such as in records of purportedly extinct birds, the records of undetected mammals consist mainly of opportunistic sightings. These species are expected to have constant sighting probability, or in some cases increasing probability due to increasing interest in finding rare species, numbers of conservation researchers, and access to isolated regions over time (Elphick et al. 2001).

We also consider the stationary Poisson model to be more reliable than the other four models in most cases because it was best corroborated by existing red-list classifications of relatively well-known species. The p values with the Poisson model were <0.05 for most extinct species; 0.05–0.1 for half of critically endangered possibly extinct species and <0.05 for the other half; and 0.1–0.4 for all critically endangered species. Thus, our results suggest that the stationary Poisson model is the better one for most species with more than four sightings.

Like the Weibull and the nonparametric models, the Cox models were prone to type II error (failing to detect extinction). When we compared the results of the stationary Poisson model with the other models, the Cox search model and the Cox century models failed to detect extinction in 40% and 72% of species with more than four sightings respectively. In the Cox regression model it is assumed that traits associated more often with previously rediscovered species will predict future rediscoveries. This is not always the case because some undetected species that share characteristics of many rediscovered species are extinct. Thus, our results indicate that Cox models do not provide reliable estimates of the probability of rediscovery in species with insufficient dated records for models of sighting distribution. However, the two Cox regression models assigned similar ranks in terms of p values to the three sighting distribution models. The probabilities of rediscovery from the Cox century model were also the only ones significantly correlated with the p values from the stationary Poisson model. Therefore, we suggest the Cox century model provides a valid rank of the relative probability of rediscovery for species with very few sightings.

Our evaluation does not account for the relative cost of types I and II errors (Field et al. 2004; Rout et al. 2010). The Cox, Weibull, and nonparametric models are more likely to fail to correctly identify extinction than the Poisson method. However, the Cox, Weibull, and nonparametric models might still be appropriate if the cost of incorrectly concluding that a species is extinct is likely to be higher than the cost of failing to detect a real extinction. For example, species-level management may cease if a species is mistakenly considered extinct, which may hasten its extirpation (Collar 1998; Fisher 2011*b*). Failing to detect a recent extinction may prolong searches, which are likely to be less costly and be shorter term (Field et al. 2004; Rout et al. 2010).

Models for Very Recent Last Sightings

The baiji and the Christmas Island pipistrelle (*Pipistrellus murrayi*) were the only undetected species in our data set with a last sighting date in this century. The last confirmed sighting of a baiji (two individuals) was in 2006 (Turvey et al. 2007). The sighting was considered reliable because the observers were familiar with the last captive specimen, which died in 2002. This extremely recent date of last sighting means the baiji would be classified as extant by the stationary Poisson model. If there were no further sightings, the baiji would be classified as extinct in 2013 with 95% confidence by the stationary Poisson model.

The baiji is classified as critically endangered by the IUCN, although its red-listed species account states, "the preponderance of evidence indicates that the baiji is very close to extinction or may already be extinct." Turvey et al. (2007) argue that it is extinct on the basis of the exceptionally intense search effort for the species. Search effort since mid 2006 was geographically comprehensive and has not detected the species. The stationary Poisson model yielded a p of 0.13 for baiji, and the Cox search model a 0% chance of rediscovery. If sighting records with chance encounters are followed by systematic search efforts, the most recent gap in detections is actually more significant than the stationary Poisson model suggests, and in these cases the model is too conservative (Solow 1993*a*). McCarthy (1998) developed a modification of this model, the partial Solow equation, to account for changes in search effort. The partial Solow equation requires a quantitative metric of search effort, such as the number of species deposited each year in museum records. The Cox model is appropriate for historical sightings with no information on past effort.

The Christmas Island pipistrelle is also classified as critically endangered. This bat was endemic to an island of 135 km^2. It was readily detected by its echolocation calls, which ceased in August 2009 (Lumsden 2009). Comprehensive and continuous search effort has failed to detect it since then. Species with very recent disappearances such as these are classified as extant by the stationary Poisson model, regardless of changes in effort, but very high effort without success implies a low chance of rediscovery in the Cox search model regardless of the length of time a species has been undetected. Thus, we propose that for species in which there has been a very large, documented increase in search effort between a recent last sighting and the present but for which there are no quantitative data on historical effort the Cox search model is the most appropriate. Our results strongly suggest that the baiji and Christmas Island pipistrelle are extinct.

Choice of Models

We propose two rules of thumb to choose among models for identifying extinction in undetected mammals. Use the results of the stationary Poisson model if there are more than four sightings in the species records. Use the Cox century model if the last sighting is very recent and there has been a well-documented substantial increase in search effort since the species disappeared. If there are too few records, species-specific estimates of the probability of rediscovery are not possible, but one could rank the relative probability of rediscovery in poorly known species with the Cox century model.

All species with more than four sightings were shown as very likely to be extinct ($p \geq 0.9$) in the Cox century model, except for Alcorn's pocket gopher (Table 1). As for North American and Hawaiian birds analyzed with the stationary Poisson model (Elphick et al. 2010), the interval between last sightings and estimated extinction for most mammals was short (1–31 years, mean = 8.8 years) (Table 1 and Supporting Information). On the basis of our rule of thumb, the most likely mammals to be rediscovered are the Montane monkey-faced bat (*Pteralopex pulchra*) and the Armenian myotis (*Myotis hajastanicus*) (both have a probability of rediscovery >80% with the Cox century model), Alcorn's pocket gopher (categorized as extinct by the stationary Poisson model; probability of rediscovery >80% with Cox century model), and Wimmer's Shrew (*Crocidura wimmeri*) (probability of rediscovery >75% according to the Cox century model) (Table 3). These are all poorly documented high-elevation or tropical forest endemics with small ranges (IUCN 2009). The critically endangered Montane monkey-faced bat is known from a single specimen collected at 1200 m asl on the island of Guadalcanal. The critically endangered and poorly known Armenian myotis is only known from females at five sites above 1800 m asl in the basin of Sevan Lake, Armenia. These are probably nursery caves, so the habitat and roost sites of males are unknown. No bats were found in a search in 2003 (IUCN 2009). Alcorn's pocket gopher is a critically endangered Mexican rodent, endemic to a small pine-oak forest around 2000 asl. It was locally abundant in 1997–1998. However, its habitat has since been largely deforested, and it was

Table 3. Relative ranked probability of rediscovery for 90 undetected mammals with fewer than five sightings on the basis of the Cox century[a] model.

Species	*Status*[b]	*Last sighting*	*Rank*[c]
Pteralopex pulchra, montane monkey-faced bat	CE	1990	1
Myotis hajastanicus, Armenian myotis	CE	1989	2
Pappogeomys alcorni, Alcorn's pocket gopher	CR	1998	3
Crocidura wimmeri, Wimmer's shrew	CE	1976	4
Mysateles meridionalis, Isla De La Juventud tree hutia	CR	1978	5
Pteropus tokudae, Guam flying fox	EX	1974	6
Crateromys australis, Dinagat bushy-tailed cloud rat	CE	1974	7
Abditomys latidens, Luzon broad-toothed rat	DD	1972	8
Myosorex eisentrauti, Eisentraut's mouse shrew	CR	1968	9
Tylomys tumbalensis, Tumbalá climbing rat	CR	1968	10
Myosorex rumpii, Rumpi mouse shrew	EN	1967	11
Hybomys basilii, Father Basilio's striped mouse	EN	1965	12
Cryptonanus ignitus, red-bellied gracile mouse opossum	EX	1962	13
Murina tenebrosa, gloomy tube-nosed bat	CE	1962	14
Zaglossus attenboroughi, Attenborough's echidna	CR	1961	15
Juscelinomys candango, Candango mouse	EX	1960	16
Tylomys bullaris, Chiapan climbing rat	CR	1968	17
Gazella bilkis, Queen of Sheba's gazelle	EX	1951	18
Chrysochloris visagiei, Visagie's golden mole	DD	1950	19
Octodon pacificus, Isla Mocha degu	CR	1959	20
Melanomys zunigae, Zuniga's dark rice rat	CE	1949	21
Crateromys paulus, Ilin bushy-tailed cloud rat	DD	1953	22
Paracoelops megalotis, Vietnam leaf-nosed bat	DD	1947	23
Uromys emmae, Emma's giant rat	CE	1946	24
Eudorcas rufina, red gazelle	DD	1936	25
Dendromus kahuziensis, Mt. Kahuzi climbing mouse	CR	1967	26
Dendromus vernayi, Vernay's climbing mouse	DD	1937	27
Lagorchestes asomatus, central hare-wallaby	EX	1932	28
Nesoryzomys darwini, Darwin's Galapagos mouse	EX	1930	29
Gazella saudiya, Saudi gazelle	EX	1936	30
Peromyscus mekisturus, Puebla deer mouse	CE	1948	31
Nilopegamys plumbeus, Ethiopian water mouse	CE	1928	32
Cryptotis nelsoni, Nelson's small eared shrew[d]	CE	1951	33
Dendrolagus mayri, Wondiwoi tree kangaroo	CE	1928	34
Zalophus japonicus, Japanese sea lion	EX	1951	35
Mesocapromys nanus, dwarf hutia	CE	1937	36
Peromyscus guardia, Angel Island mouse	CE	1991	37
Calcochloris tytonis, Somali golden mole	DD	1964	38
Leporillus apicalis, lesser stick-nest rat	CE	1933	39
Lagostomus crassus, Peruvian plains vizcacha	EX	1910	40
Nyctophilus howensis, Lord Howe long-eared bat	CE	1915	41
Nyctimene sanctacrucis, Nendo tube-nosed bat	DD	1907	42
Cryptochloris wintoni, De Winton's golden mole	CE	1907	43
Rattus nativitatis, bulldog rat	EX	1903	44
Harpiola grisea, Peter's tube-nosed bat	DD	1904	45
Mesocapromys sanfelipensis, little earth hutia	CE	1978	46
Notomys amplus, short-tailed hopping mouse	EX	1896	47
Uromys imperator, emperor rat	CE	1887	48
Pharotis imogene, Thomas's big-eared bat	CE	1890	49
Peromyscus pembertoni, Pemberton's deer mouse	EX	1931	50
Neotoma bunkeri, Bunker's woodrat	EX	1931	51
Thallomys shortridgei, Shortridge's rat	DD	1922	52
Neotoma martinensis, San Martin Island woodrat	EX	1925	53
Neotoma anthonyi, Anthony's woodrat	EX	1926	54
Pteropus aruensis, Aru flying fox	CE	1867	55
Uromys porculus, Guadalcanal rat	CE	1888	56
Oryzomys nelsoni, Nelson's rice rat	EX	1897	57
Pipistrellus sturdeei, Bonin pipistrelle	DD	1891	58
Leimacomys buettneri, groove-toothed forest mouse	DD	1890	59
Pteropus brunneus, dusky flying fox	EX	1874	60
Oryzomys antillarum, Jamaican rice rat	EX	1877	61

continued

Table 3. (continued)

Species	*Status*[b]	*Last sighting*	*Rank*[c]
Notomys longicaudatus, long-tailed hopping mouse	EX	1901	62
Oligoryzomys victus, St Vincent pigmy rice rat	EX	1892	63
Nesophontes micrus, western Cuban island-shrew	EX	1650	64
Boromys torrei, Torre's cave rat	EX	1500	65
Nesophontes paramicrus, St Michael island-shrew	EX	1500	66
Neovison macrodon, sea mink	EX	1880	67
Megalomys luciae, Santa Lucia giant rice rat	EX	1852	68
Plagiodontia ipnaeum, Samana hutia	EX	1500	69
Isolobodon portoricensis, Puerto Rican hutia	EX	1525	70
Boromys offella, Oriente cave rat	EX	1600	71
Bettongia pusilla, Nullarbor dwarf bettong	EX	1500	72
Isolobodon montanus, montane hutia	EX	1600	73
Brotomys voratus, mohuy	EX	1570	74
Solenodon marcanoi, Marcano's solenodon	EX	1500	75
Nesophontes major, major island-shrew	EX	1500	76
Cuscomys oblativa, Machu Pichu chinchilla rat	EX	1600	77
Pteropus pilosus, large Palau flying fox	EX	1873	78
Heteropsomys insulans, insular cave rat	EX	1500	79
Hexolobodon phenax, imposter hutia	EX	1600	80
Nesophontes zamicrus, Haitian island-shrew	EX	1600	81
Pseudomys gouldii, Gould's mouse	EX	1857	82
Desmodus draculae, giant vampire bat	EX	1500	83
Cryptoprocta spelea, giant fossa	EX	1500	84
Megaoryzomys curioi, Galapágos giant rat	EX	1600	85
Nesophontes edithae, Edith's island-shrew	EX	1500	86
Notomys mordax, Darling downs hopping mouse	EX	1845	87
Geocapromys columbianus, Cuban coney	EX	1500	88
Potorous platyops, broad-faced potoroo	EX	1875	89
Notomys macrotis, big-eared hopping mouse	EX	1843	90

[a] *Cox proportional hazards model with a data set including the 19th, 20th, and 21st centuries, but excluding search effort and species not seen since before the 19th century.*
[b] *The 2009 IUCN Red List categories (status): EX, extinct; DD, data deficient; CE, critically endangered (possibly extinct); CR, critically endangered; EN, endangered.*
[c] *Rank 1 implies the greatest probability of rediscovery and rank 90 the least.*
[d] *This species has been recently rediscovered (Cervantes & Guevara 2010).*

subject to targeted killing by local farmers. Searches of the species' range since 2001 have not detected it (Demastes et al. 2003; IUCN 2009). Wimmer's shrew is a poorly known rainforest species in southern Côte d'Ivoire with two dated sightings, the last in 1978. It is listed as critically endangered possibly extinct because all habitat for this species in the known range has apparently been cleared for agriculture (IUCN 2009).

These species highlight the point that assuming extinction in undetected and poorly known species is likely to hasten their extirpation if it prevents habitat protection (Collar 1998). In a forest remnant in the Philippines, the only population of the Cebu Flowerpecker (*Dicaeum quadricolor*) was unnoticed and unprotected for decades because the bird was assumed to be extinct. Like the Cebu Flowerpecker, the Montane monkey-faced bat, Armenian myotis, Alcorn's pocket gopher, and Wimmer's Shrew, other highly endangered species ranked near the top of Table 3 are currently threatened with extinction by a lack of habitat protection and other factors. A first step toward protecting these species is finding any surviving populations. A combination of Solow's stationary Poisson model and the Cox regression model allows the prioritization of search effort according to quantitative predictions of which species are most likely to be rediscovered.

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Supporting Information

Lists of mammal species categorized as extinct by all our models (Appendix S1), categorized as extant by all our models (Appendix S2), and categorized as extinct by some, but not all our models (Appendix S3) and a table

listing the dates of last recorded sightings of missing and extinct mammals that have a sighting record of at least three occasions (Appendix S4) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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